

Behavioural Responses of Two Native Australian Fish Species (*Melanotaenia duboulayi* and *Pseudomugil signifer*) to Introduced Poeciliids (*Gambusia holbrooki* and *Xiphophorus helleri*) in Controlled Conditions

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Experimental treatments to compare behavioural responses included native fish species only, natives plus one exotic species and natives plus both exotic species. The mosquitofish, *Gambusia holbrooki* frequently attacked both native species, but tended to nip *Melanotaenia duboulayi* (especially small individuals) and chase *Pseudomugil signifer*. The frequency of attacks by *G. holbrooki* on *M. duboulayi* rose when all four fish species were present. When food was added, all four species showed a strong increase in aggression, especially in the four-species treatment, where there were significant increases in the frequency of attacks by the swordtail *Xiphophorus helleri* on *M. duboulayi* and by *M. duboulayi* on *G. holbrooki*, and of conspecific attacks by *M. duboulayi*. Increased attack frequency was associated with aggregation closer to the water's surface, regardless of the presence of food. The results support the hypothesis that introduced poeciliids can have deleterious competitive effects on native species. However, while juvenile *M. duboulayi* were particularly vulnerable to the secondary effects of fin-nipping, *P. signifer* appeared to be more susceptible to physical displacement and reduced food capture success.

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INTRODUCTION

Prominent among the species of freshwater fish that have been introduced to Australia are the poeciliids *Gambusia holbrooki* (mosquitofish) and *Xiphophorus helleri* (swordtail). *Gambusia holbrooki* is widespread and prolific throughout much of Australia (Arthington 1991). *Xiphophorus helleri* is locally abundant in south-eastern Queensland (Arthington et al. 1983, McKay 1989, McDowall 1996), and there is a strong chance of further spread of this species in tropical and subtropical Australia (Arthington 1991).

Expanding ranges of introduced fishes and widespread declines of native populations have heightened interest in interactions between non-indigenous and resident species. Although the underlying mechanisms have been poorly documented, it is likely that *Gambusia* species exert diverse effects

on other fish through interference competition, resource competition and predation (Lloyd 1990). *Gambusia holbrooki* are aggressive towards other species, and damage to fins and scales resulting from nipping by *G. holbrooki* (Lloyd 1987; Howe et al. 1997), coupled with secondary infection, can prove fatal. Such aggressive behaviour by *Gambusia* may cause physiological stress, and in topminnows (*Poeciliopsis occidentalis*) it leads to reduced rates of feeding, fecundity and survival (Schoenherr 1981). *Gambusia holbrooki* may also consume the larvae of *Pseudomugil signifer*, melanotaeniids (rainbowfishes) and other Australian native fish species (Aarn & Ivantsoff 2001).

The ecological impacts of *X. helleri* are poorly understood (Arthington 1991). *Xiphophorus helleri* is primarily herbivorous (Arthington et al. 1983; Arthington 1989) and its diet is likely to overlap more with small omnivores (e.g. *Melanotaenia duboulayi*,

Arthington 1992) than insectivorous carnivores (e.g. *P. signifer*). *Xiphophorus helleri* can occur at very high densities in shallow Australian creeks (pers. obs.), and it is possible that this may lead to enhanced interspecific resource competition through the local depletion of invertebrate prey. *Xiphophorus helleri* and *G. holbrooki* often co-occur (Arthington et al. 1983), and the pressure of high numbers of these two species together could subject native species to significant stress (McKay 1978, cited by Arthington 1991; Howe et al. 1997).

Several groups of Australian native fish tend to occur in much lower numbers in the presence of *G. holbrooki* (Arthington et al. 1983; Lloyd 1990), but further work is necessary to disentangle the impacts of introduced species from the effects of habitat modification (Arthington 1991). To this end, there is a clear need for behavioural analyses of interspecific interactions (Lloyd 1990), which are likely to vary with the species involved (Arthington & Lloyd 1989). In particular, because the impact of such interactions tends to be more severe in confined or still water environments (Pen and Potter 1991) and when the native fish are relatively small, it is important to gather comparative information on the effects of density and body size (Howe et al. 1997).

The present study investigated the behavioural responses of *Melanotaenia duboulayi* (Family Melanotaeniidae) and *Pseudomugil signifer* (Family Pseudomugilidae) to *Gambusia holbrooki* and *Xiphophorus helleri* (Family Poeciliidae). Melanotaeniids and pseudomugilids are speciose and abundant in tropical inland waters in the Australia / Papua New Guinea region (McDowall 1996). However, although *M. duboulayi* and *P. signifer* are the commonest representatives of these groups in south-eastern Queensland streams, they have been driven to very low densities in disturbed habitats that support large populations of introduced poeciliids (Arthington et al. 1983). To assess the relative competitive potential of *M. duboulayi* and *P. signifer* in the presence of *G. holbrooki* and/or *X. helleri*, we tested the prediction that the frequency of chasing, fin nipping and displacement of the native species would increase in the presence of the exotics - especially when food was available, when both exotic species were present, and when the body size of the native individuals was relatively small.

MATERIALS AND METHODS

On several occasions in winter (May-September) 1998, fish were collected from a site in Moggill Creek, Brisbane, using bait traps and a seine

net. Individuals of these four species were transferred to a laboratory at the University of Queensland, where they were maintained in filtered, single-species aquaria (tank volume 0.05 m³; c. 50 fish per tank) for 1-3 weeks prior to experimentation. During this time they were fed on a commercial fish flake diet, which was the food used in the experiments. The tanks were filled with aged tapwater and maintained under artificial light (L:D 12:12) at a constant temperature of 23 °C

Experiment 1. : Effects of species composition on behavioural interactions.

Experimental trials were conducted in May and September 1998 in a 90 litre tank (1.5 x 0.5 x 0.35m) maintained under the same conditions as the holding tanks. Grid markings on the tank allowed the vertical height in the water column of the fish to be estimated. The tank was screened by black plastic sheeting to avoid external visual bias and an eye slit was cut into the sheet to allow observations.

In these trials, mixed species groups totalling 20 fish were used and individuals were used only once. The ratio of mean catch rates from repeated sampling at the field site (7:3:6:4 for *M. duboulayi*, *P. signifer*, *G. holbrooki* and *X. helleri* respectively) was used as a guide when determining the relative numbers of fish in the four treatments (Table 1). The treatments were as follows: Treatment 1, native species; Treatment 2, native species plus *X. helleri*; Treatment 3, native species plus *G. holbrooki*; Treatment 4, native species plus both exotic species.

Attempts were also made to equalise sex ratios and to ensure that the fish used in each trial were of a representative range of sizes. Fish biomass was not measured directly but on average the aggregate total length of the fish used (all species combined) was 55.6 cm, 58.4 cm, 50.0 cm and 53.4 cm for Treatments 1 to 4, respectively. The order of trials was randomised with respect to treatment, and ten replicate trials were performed for each treatment.

In each trial, the fish were placed in the tank and left to settle for 15 minutes. This was followed by a period of focal sampling (Martin and Bateson 1990) to record the behaviour of individual fish: a randomly selected fish of each species was watched for two minutes, during which time its depth was recorded every 20 seconds by reference to the markings on the tank. This was followed by a five-minute sampling period in which the occurrence and direction of all agonistic interactions (chases, nips) involving a randomly chosen focal individual were recorded. A single fish flake was then placed on the water's surface in the central, intermediate depth section of the tank and the above procedure, involving both periods of focal sampling, was repeated. Pilot studies indicated

Table 1. Summary of experiments and treatments with mean (±SE) total length (excluding tail sword of *X.helleri*) and numbers of individuals.

Species / size group	Mean length (cm)	SE	Expt	Treatment					
				1	2	3	4	5	6
<i>X. helleri</i>									
Mixed	3.39	0.25	1		6		4		
Small	2.50	0.13	2	8					12
Large	4.50	0.11	2		8			12	
<i>M. duboulayi</i>									
Mixed	3.07	0.15	1	14	9	9	7		
Small	2.61	0.11	2		12		11		
Large	3.89	0.20	2	12		11			
<i>P. signifer</i>									
	2.10	0.07	1	6	5	4	3		
	2.10	0.07	2					8	8
<i>G. holbrooki</i>									
	2.00	0.05	1			7	6		
	2.00	0.05	2			9	9		

that a single food source was sufficient to elicit behavioural responses in all fish, while promoting competition. Each trial therefore yielded data on aggressive encounters and the depth of the species concerned, both in the absence and presence of food. Treatment differences in mean chasing frequency, mean nipping frequency and mean depth were examined using analysis of variance and multiple range (Tukey) tests, separate analyses being carried out on the “food absent” and “food present” data. Primary data (numbers of nips and chases) were standardised by dividing the number of attacks received by focal fish per trial by the number of potential aggressors. For interspecific attacks the number of aggressors was n, where n = group size for the attacking species. For conspecific attacks the number of aggressors was n-1. Data were log-transformed prior to analysis since means and standard deviations were linearly related.

Experiment 2. Effects of fish size on interspecific interactions.

This experiment was designed to investigate the impact of relative body size on interspecific interactions. *Melanotaenia duboulayi* and *X. helleri* were each divided on the basis of body size into two groups (large and small) (Table 1). Because *P. signifer* and *G. holbrooki* are relatively small species, only one size class (adult fish, which were similar in size to small *M. duboulayi* and *X. helleri*) were used. There were six mixed-species treatments, as follows: Treatment 1, large *M. duboulayi*, small *X. helleri*; Treatment 2, small *M. duboulayi*, large *X. helleri*; Treatment 3, large *M. duboulayi*, *G. holbrooki*;

Treatment 4, small *M. duboulayi*, *G. holbrooki*; Treatment 5, *P. signifer*, large *X. helleri*; Treatment 6, *P. signifer*, small *X. helleri*. Table 1 gives numbers of fish used in the different treatments. There were seven replicate trials for each treatment. The focal sampling and data analysis procedures were as described for Experiment 1. Separate analyses were carried out to compare the *M. duboulayi* treatments (1-4) and the *P. signifer* treatments (5-6).

RESULTS

Experiment 1

Aggressive encounters

There were several statistically significant between-treatment differences in attack frequency (Fig.1; Table 2). Two main trends were apparent, namely:

- (a) Attack levels were significantly higher with the combined treatment (Treatment 4) than the other treatments. A notable exception to this trend occurred in the case of chasing of *G. holbrooki* by *P. signifer*, where the mean frequency for Treatment 3 was marginally significantly higher than that for Treatment 4 ($F_{1,18} = 3.99$; $p = 0.061$).
- (b) Significant treatment differences occurred in the presence of food. The only exception here involved attacks by *G. holbrooki* on *M. duboulayi*, where although the difference

between treatment means for nipping was only marginally significant in the presence of food ($F_{1,18} = 4.12$; $p=0.057$), treatment means for chasing varied significantly in the absence of food (Table 2).

Table 3 summarises total attack frequency, the frequency of nips relative to chases, and total attack frequency in the presence of food relative to that in the absence of food. The following trends were clear:

- (a) On a standardised per capita basis, *M. duboulayi* received more attacks than the other species. Most of these came from *G. holbrooki* but conspecific attacks by *M. duboulayi* were also relatively common. In contrast, attacks on *P. signifer* were less frequent and were mainly conspecific in nature.
- (b) Attacks by *G. holbrooki* on *M. duboulayi* mainly involved nipping. Other interspecific and conspecific attacks were dominated by chasing.
- (c) The addition of food increased attack frequency. Food addition had a greater relative impact on attacks by *X. helleri* than on attacks by the other species, but absolute levels of aggression by *X. helleri* were very low. Observations indicated that *X. helleri* were territorial and defended localised areas of the tank. Attacks by *M. duboulayi* on conspecifics and on *P. signifer* also increased markedly in relative terms.

Depth preferences

The four species tended to swim at different depths, with *P. signifer* nearest the surface, followed

by *G. holbrooki*, *M. duboulayi* and *X. helleri* in order of increasing depth (Fig. 2). However, in the presence of food, *P. signifer* moved deeper while *G. holbrooki* moved closest to the surface. The addition of food had little impact on the preferred depth of *M. duboulayi*, but it affected *X. helleri* differently depending on treatment: when *X. helleri* was alone with the native species, its mean depth increased, but when *G. holbrooki* was also present, the mean depth of *X. helleri* decreased (Fig. 2).

For *P. signifer*, *G. holbrooki* and *M. duboulayi* there was a consistent effect of treatment, individuals of all these species moving closer to the surface in

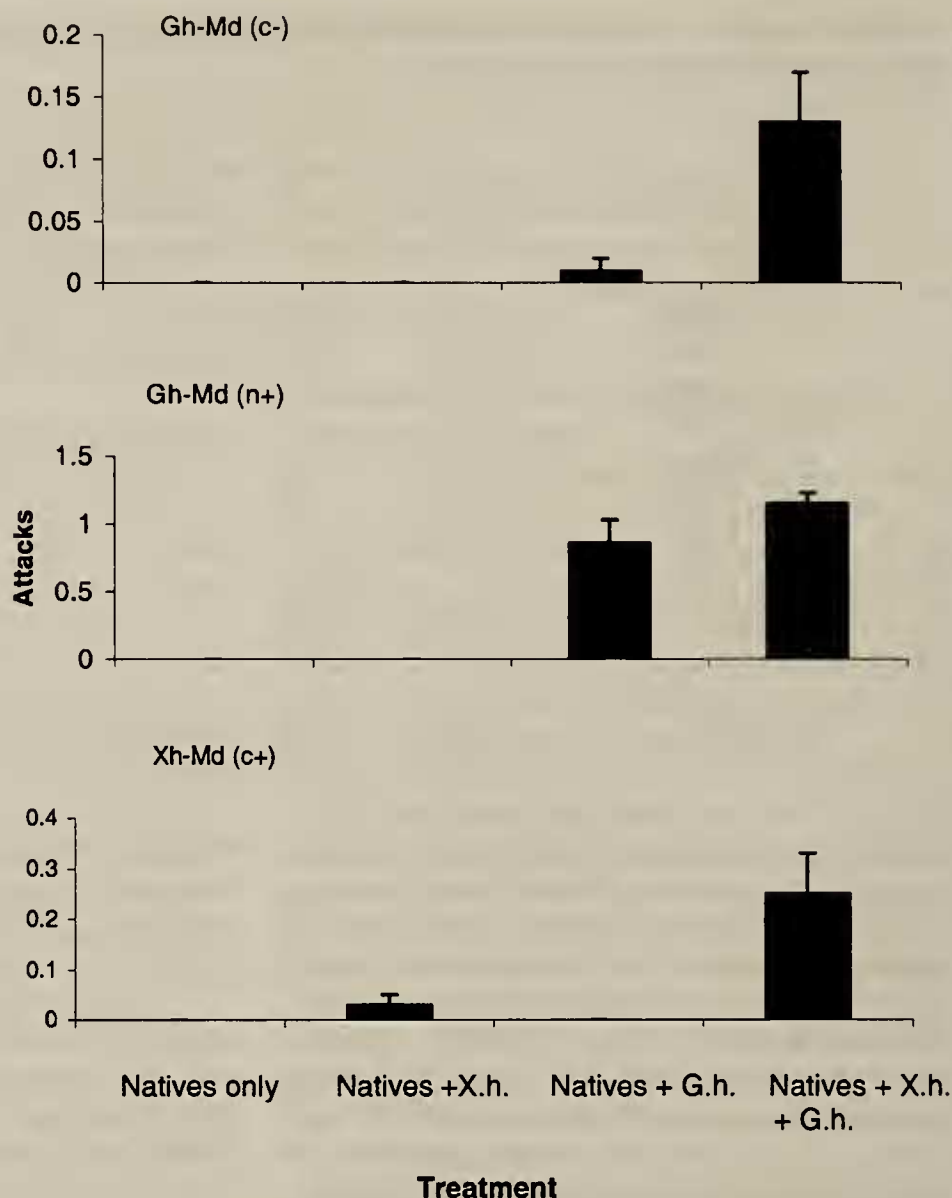


Figure 1a. Standardised (per capita) attack frequencies per trial. Bars represent means and standard errors. c, chases; n, nips; -, no food; + food added. Species names are abbreviated (see caption for Table 2); the first-named of each pair is the attacking species. Attacks by exotic and native species are shown in Fig. 1(a), above, and Fig. 1(b), facing page, respectively.

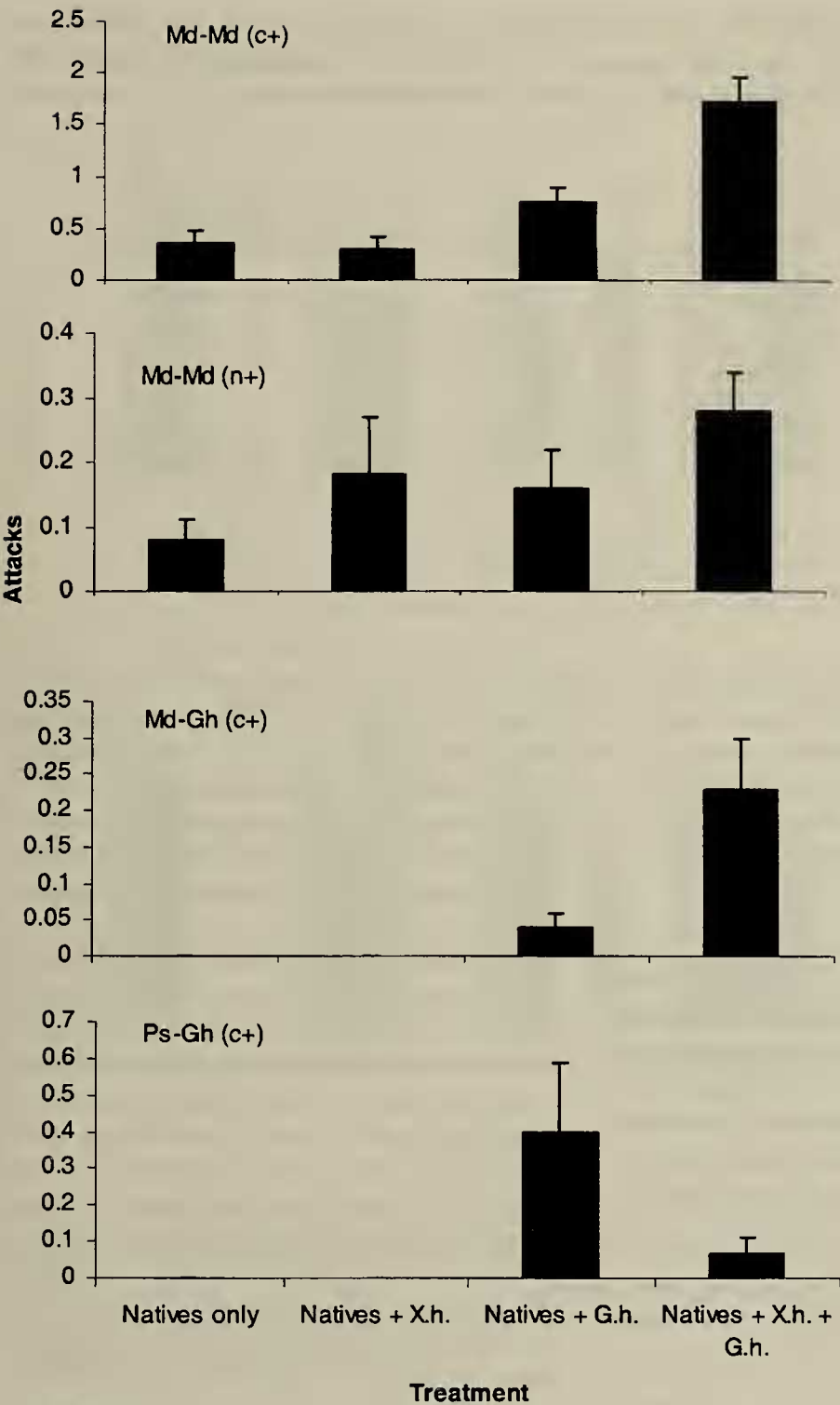


Figure 1b.

Treatment 4 (i.e., when both *G. holbrooki* and *X. helleri* were present; Fig. 2). However, between-trial variation was high and these trends were only marginally significant ($F_{1,18} = 4.51$, $p = 0.048$ for *M. duboulayi*; $F_{1,18} = 4.11$, $p = 0.058$ for *P. signifer*; comparisons of Treatments 1 and 4 in the absence of food).

Feeding success

Individual *M. duboulayi* tended to take food before individuals of the other species (Table 4). Overall, *X. helleri* had a lower per capita feeding success than the other species.

Experiment 2

Larger individuals of *M. duboulayi* were significantly less susceptible to attack by *G. holbrooki*. In the presence of food, *G. holbrooki* chased small *M. duboulayi* approximately six times more often than large *M. duboulayi*, and *G. holbrooki*-small *M. duboulayi* chases were significantly more frequent than those for the other three combinations of *M. duboulayi* and exotic species ($F_{3,24} = 6.74$; $p = 0.0019$). Similarly, there were significant differences between treatments in terms of the frequency of nips on *M. duboulayi* ($F_{3,24} = 34.75$, $p = 0.0001$), with small *M. duboulayi* being nipped by *G. holbrooki* about eight times more frequently than were large *M. duboulayi*. Attacks by *X. helleri* on *P. signifer* and *M. duboulayi* were infrequent and not significantly affected by the relative size of *X. helleri*.

When offered food and mixed with *G. holbrooki*, large *M. duboulayi* spent significantly more time in the deep section of the tank than did smaller individuals ($F_{3,24} = 4.54$, $p = 0.012$). There were no significant differences in tank usage with respect to depth between the treatments with natives plus *X. helleri*.

DISCUSSION

The results supported the prediction that the addition of food and the number of exotic species present would positively influence the frequency of attacks on the native species. In most cases, the highest attack rates were recorded when all four species were present, and most significant treatment differences occurred in the presence of food. Food has been shown to increase rates of aggression in other fish species (Syarifuddin & Kramer 1996). It is noteworthy that, although *G. holbrooki* was responsible for most interspecific attacks, chasing and nipping of *M. duboulayi* by *X. helleri* also increased to relatively high levels in the four-species treatment. The species enhancement

Table 2. Main between-treatment differences in attack frequency. Species names have been abbreviated (see key); the first-named of each pair is the attacking species. Underlined treatments are not significantly different. Key to abbreviations: Gh = *Gambusia holbrooki*; Md = *Melanotaenia duboulayi*; Ps = *Pseudomugil signifer*; Xh = *Xiphophorus helleri*

Interaction	Type of attack	Food / no food	F	df	p	Treatment differences
Gh - Md	chases	No food	7.46	1,18	0.014	T4 > T3
Gh - Md	nips	Food	4.12	1,18	0.057	T4 > T3
Xh - Md	chases	Food	5.10	1,18	0.037	T4 > T2
Md - Md	chases	Food	11.57	3,36	0.0001	T4>T3> <u>T1>T2</u>
Md - Md	nips	Food	2.90	3,36	0.048	T4> <u>T2>T3>T1</u>
Md - Gh	chases	Food	5.26	1,18	0.034	T4 > T3
Ps - Gh	chases	Food	3.99	1,18	0.061	T3 > T4

effect was associated with aggregation involving vertical movement toward the surface. When all four species were present in low numbers there was a general tendency (for all species except *X. helleri* in the absence of food) to move closer to the surface. By increasing the local density of fish, such aggregation

Table 3. Frequency of attacks (summary table). ‘Total attacks’ refers to nips plus chases. For each species combination, the ratio of nips to chases and the ratio of total attacks during all food trials to total attacks during all non-food trials are also shown. (+) indicates an increase in the presence of food, but where a ratio cannot be calculated due to a zero “no food” value. Species names have been abbreviated (see caption for Table 2).

Interaction	Total attacks/ trial	Nips : chases	Food : no food
Gh → Md	1.57	2.73	6.45
Gh → Ps	0.60	0.86	4.41
Xh → Md	0.26	0.82	24.50
Xh → Ps	0.08	1.00	(+)
Md → Md	1.06	0.24	9.34
Md → Ps	0.08	0.23	9.67
Ps → Md	0.14	0.46	(+)
Ps → Ps	0.79	0.16	3.59
Md → Gh	0.21	0.52	(+)
Md → Xh	0.05	1.00	1.33
Ps → Gh	0.49	0.56	3.41
Ps → Xh	0.04	(+)	(+)

appeared to promote elevated levels of activity and more aggressive interactions. The broader diversity of species-specific behaviours and salient stimuli may also have encouraged heightened levels of activity. In a study of conspecific and interspecific interactions between brook trout, *Salvelinus fontinalis*, and rainbow trout, *Salmo gairdneri* (= *Oncorhynchus mykiss*), Newman (1956) postulated that the presence of food increased feeding activity, which in turn increased aggressive activity as the focus of attacks was displaced from food to fellow fish of both species. He noted that feeding fish displayed some movements that are associated with aggression, such as body undulations, swift darting and biting, and suggested that such movements constituted sign stimuli eliciting attacks from other fish. The increased excitement associated with the four-species treatment (Treatment 4) could not be explained in terms of the total number of fish, which remained constant across treatments. Treatment 4 had the lowest numbers of individuals of each of the four species studied. Working with gouramis (*Trichogaster trichopterus*), Syarifuddin & Kramer (1996) found that fish were more aggressive in smaller groups and attributed this to greater costs of contest competition with increasing group size. In the present study it is possible that fish were responding more to the numbers of individuals belonging to each species than to the size of the group as a whole, but testing this hypothesis would require more work.

The four species exhibited considerable variation in the extent and type of aggression displayed. Although *M. duboulayi* were often attacked by *G. holbrooki*, they concentrated

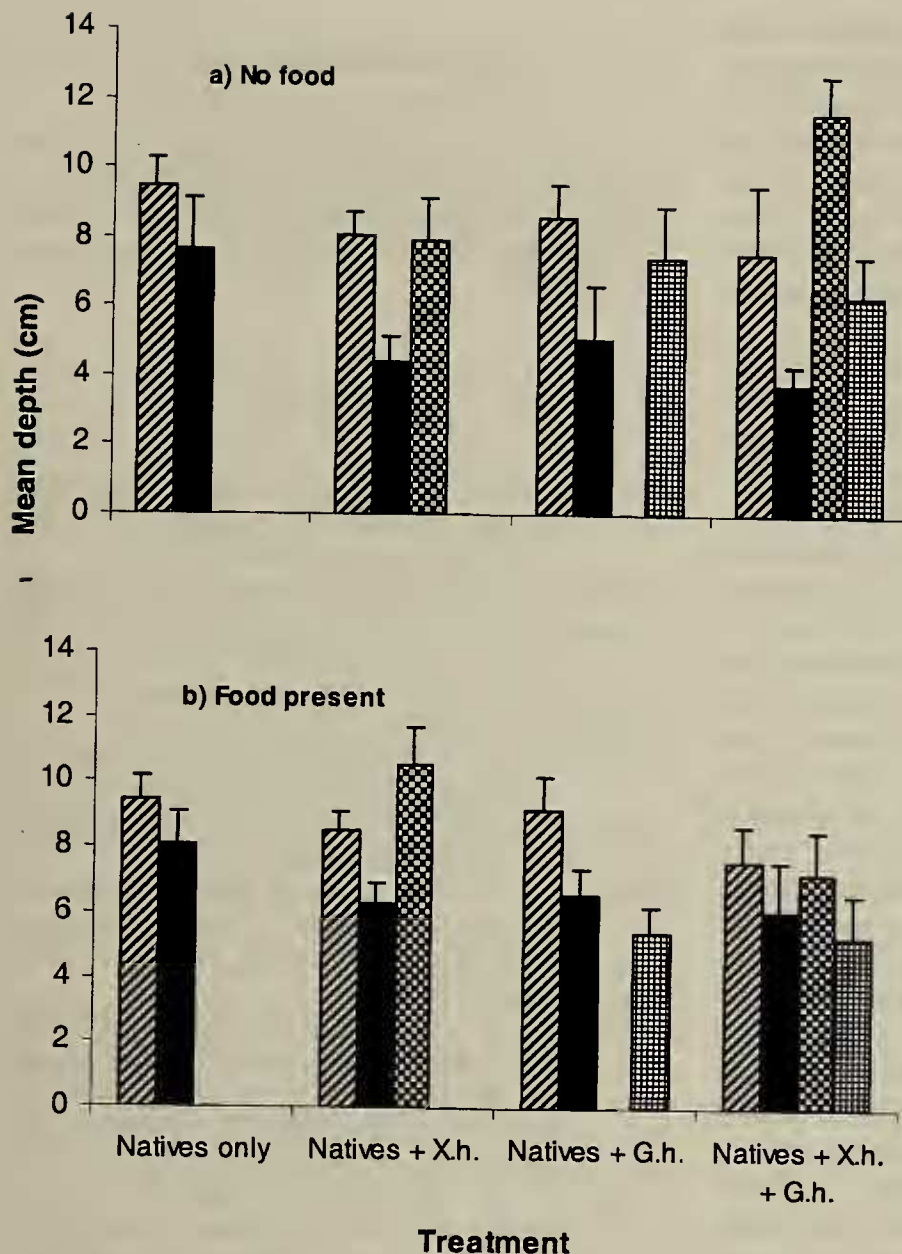


Figure 2. Mean ($\pm$ SE) swimming depths (in cm) by fish species, treatment and the absence or presence of food.. *M. duboulayi*, oblique bars; *P. signifer*, black bars; *X. helleri*, crossed oblique bars; *G. holbrooki*, crossed vertical/horizontal bars. Exotic species names are abbreviated (see caption for Table 2).

mainly on conspecific rather than interspecific exchanges. In Experiment 1, attacks by *G. holbrooki* on *M. duboulayi* were over 2.5 times more frequent than attacks by *G. holbrooki* on *P. signifer*. Further, *G. holbrooki* tended to nip *M. duboulayi* but chase *P. signifer*. However, these differences were not due simply to the difference in body size between the two native species, since in Experiment 2 *G. holbrooki* attacked small *M. duboulayi* more readily than large *M. duboulayi*. Juvenile *M. duboulayi* therefore appear to be particularly susceptible to nipping.

The depths occupied by the four species examined were a function of (a) species- and size-specific differences in mean depth preference, (b) an increased tendency to aggregate near the surface as species diversity increased, and (c) species-specific changes in depth in response to the addition of food. In the absence of food, *P. signifer* occurred closest to the surface. However, when food was present, *G. holbrooki* moved closest to the surface while *P. signifer* retreated toward the deeper regions of the tank. These results suggest that *P. signifer* is a relatively poor competitor for food at the surface, as does the fact that for *P. signifer* (unlike *M. duboulayi*, *X. helleri* and *G. holbrooki*) feeding success was lowest when all four species were present.

Table 4. Per capita feeding success of the four species. In this table the percentage of trials when any member of a given species took the offered food before members of any other species has been divided by the number of individuals of the focal species. Species names have been abbreviated (see caption for Table 2).

Species	Treatment			
	1	2	3	4
	Natives only	Natives + X.h.	Natives + G.h.	Natives + X.h. +G.h.
Md	6.6	8.9	6.4	8.7
Ps	1.2	4.0	4.5	1.0
Xh	-	0	-	2.8
Gh	-	-	3.4	4.2

In Experiment 2, larger *M. duboulayi* were less attracted to the shallow part of the tank than were smaller *M. duboulayi*. In the wild, adult *M. duboulayi* tend to occur at greater depths than juveniles and are less inclined to feed at the surface (Hattori and Warburton, in press). These observations may reflect the general tendency for small fish species, and small individuals within species, to occur closer to the surface (Helfman et al. 1997).

There are substantial overlaps among the four focal species in terms of habitat use and diets (Arthington et al. 1983; Arthington 1992), so that the potential exists for interspecific competition. Further, in disturbed urban streams invaded by exotic semiaquatic grasses the extent of open flowing water habitats preferred by *M. duboulayi* and *P. signifer* is typically reduced (Arthington et al. 1983), and the success of these species will depend more heavily on their ability to utilise the low velocity grassy edge habitats favoured by poeciliids. Similarly, the prerequisites for competition exist when mixed populations of native and exotic species are trapped in shrinking ponds during droughts (Howe et al. 1997). Although the present laboratory-based findings should not be applied in a precise predictive way to wild populations, they do illustrate behavioural mechanisms by which exotic fish species may negatively impact on natives under confined conditions in streams and ponds. Where exotic species occur at high density, and especially where *G. holbrooki* and *X. helleri* coexist, associated increases in activity and aggression are likely to lead to elevated stress levels, increased energy expenditure, reduced attentiveness to foraging and anti-predator vigilance, and reduced per capita feeding success in the native species. More research is required on how dynamic behavioural interactions between shoaling fish species affect the composition of local stream assemblages. There is also a need for allied work on the effects of variation in abundance ratios, food availability, temperature and cover on behaviour.

In summary, in laboratory experiments the behaviour of *G. holbrooki* had clear, species-specific impacts on *M. duboulayi* and *P. signifer*. *Gambusia holbrooki* was responsible for both direct aggression and displacement, but it also encouraged increased activity and aggression by other species, including *X. helleri*. The presence of multiple exotic species may therefore exacerbate the negative impact of high poeciliid densities on native species such as *M. duboulayi* and *P. signifer*.

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